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Running Title: Climate and shrubline advance

Climate warming as a driver of tundra shrubline advance

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Key-words. shrub, alpine, tundra, high-latitude, range expansion, recruitment, age distributions,
climate, willow (*Salix*), Yukon

Tweetable Abstract. Shrubs advance into northern alpine tundra as climate warms: summer
temperature influences growth; winter temperature influences recruitment

Summary

1. Climate warming is predicted to alter ecological boundaries in high-latitude ecosystems including the elevational or latitudinal extent of tall shrubs in Arctic and alpine tundra. Over 60 studies from 128 locations around the tundra biome have investigated shrub expansion in tundra ecosystems; however, only six studies test whether shrublines are actually advancing up hill-slopes or northward into tundra where tall shrubs are currently absent.

2. We test the hypothesis that willow shrublines have expanded to higher elevations in relation to climate across a 50 x 50 km area in the Kluane Region of the southwest Yukon Territory, Canada by surveying of 379 shrubs at 14 sites and sampling of 297 of the surveyed shrubs at 10 sites. We compared growth and recruitment to climate variables to test the climate sensitivity of shrub increase using annual radial growth analysis, age distributions and repeat field surveys to estimate the current rate of shrubline advance.

3. We found consistent and increasing rates of recruitment of alpine willows, with estimates of faster advancing shrublines on shallower hill-slopes. Mortality was extremely low across the elevation gradient. Aspect, elevation and species identity did not explain variation in recruitment patterns, suggesting a regional factor, such as climate, as the driver of the observed shrubline advance.

4. Annual radial growth of willows was best explained by variation in summer temperatures, and recruitment pulses by winter temperatures. Measured recruitment rates are $\sim 20 \pm 5$ individuals per hectare per decade (mean \pm SE) and measured rates of increased shrub cover of $\sim 5 \pm 1$ % per decade (mean \pm SE) measured at the Pika Camp site between field surveys in 2009 and 2013. Our results suggest that shrubline will continue to advance over the next 50 years, if growing conditions remain suitable. However, if future conditions differ between summer and winter seasons, this could lead to contrasting trajectories for recruitment versus growth, and influence the vegetation change observed on the landscape.

Synthesis. Our findings in the context of a review of the existing literature indicate that elevational and latitudinal shrublines, like treelines, are advancing in response to climate warming; however, the trajectories of change will depend on the climate drivers controlling recruitment versus growth.

51 **Introduction**

52 Species distributions are expected to track climate at the global scale (Gaston 2009), and tundra
 53 ecosystems are an excellent place to test for climate-induced range expansion, as the tundra biome
 54 is climate constrained and experiencing the most rapid change of any terrestrial biome on the planet
 55 (Post *et al.* 2009). Climate warming has already altered ecological boundaries in high-latitude
 56 ecosystems, and is thought to have contributed to the expansion of at least half of treelines into
 57 Arctic and alpine tundra globally (Harsch *et al.* 2009). Beyond the treeline, tall-statured shrub
 58 species are projected to expand their ranges with climate warming into previously low-statured
 59 tundra communities (Post *et al.* 2009; Myers-Smith *et al.* 2011a), hereafter referred to as shrubline
 60 advance. Though we have ample evidence of treeline advance from sites around the world (Harsch
 61 *et al.* 2009), an advancing shrubline in northern alpine tundra has been reported in only a few
 62 studies (Dial *et al.* 2007, 2016; Hallinger, Manthey & Wilmking 2010; Upshall 2011; Rundqvist *et*
 63 *al.* 2011) Wipf, Rixen and Stoeckli *op. cit.*, Fig. 1). In tundra ecosystems, advance of the shrubline
 64 ecotone will alter albedo, soil temperatures, nutrient turnover times, carbon cycling and
 65 biodiversity, which could create feedbacks to future shrub expansion and Arctic warming (Myers-
 66 Smith *et al.* 2011a; Pearson *et al.* 2013; Williamson *et al.* 2016). Thus, it is necessary to understand
 67 the rates and drivers of shrubline advance, in addition to increased shrub growth and recruitment, to
 68 project future vegetation change in tundra ecosystems and resulting feedbacks to ecosystem
 69 functions with warming.

70

71 Tundra ecosystems have been dominated by woody vegetation in the past (Higuera *et al.* 2008) and
 72 there is ample evidence that shrub expansion is currently underway at sites across the tundra biome
 73 (Fig. 1, Myers-Smith *et al.* 2011a). Paleoecological records indicate that shrub species were much
 74 more abundant in high-latitude ecosystems during the warmer and wetter period of the early
 75 Holocene (Higuera *et al.* 2008). Recent observations from sites around the Arctic indicate a
 76 transition towards more dense shrubland (Sturm, Racine & Tape 2001; Tape, Sturm & Racine 2006;

77 Forbes, Macias-Fauria & Zetterberg 2010; Myers-Smith *et al.* 2011a; Macias-Fauria *et al.* 2012;
 78 Ropars & Boudreau 2012; Tremblay, Lévesque & Boudreau 2012; Lantz, Marsh & Kokelj 2013;
 79 Frost & Epstein 2014; Naito & Cairns 2015). And, future climate warming in tundra ecosystems is
 80 projected to again lead to deciduous tree or shrub dominated tundra (Swann *et al.* 2010; Pearson *et*
 81 *al.* 2013). However, evidence is lacking for advances of shrubline ecotones up hill-slopes in
 82 mountain regions or northward into the Arctic, as most studies instead test for changes in the cover
 83 or abundance of tundra shrubs (Fig. 1).
 84
 85 Climate is linked to the position of the shrubline ecotone (Lantz, Gergel & Kokelj 2010b) and is
 86 often invoked as the cause of tree or shrubline advance (Truong, Palmé & Felber 2007; Harsch *et*
 87 *al.* 2009; Hallinger *et al.* 2010). Experimental studies also indicate that warming will increase the
 88 dominance of shrub species in tundra ecosystems (Arft *et al.* 1999; Walker *et al.* 2006; Elmendorf
 89 *et al.* 2012a), and this is corroborated by observations of greater shrub increases at sites that have
 90 experienced greater warming (Elmendorf *et al.* 2012b). Shrub growth has been demonstrated to be
 91 climate sensitive (Forbes *et al.* 2010; Hallinger *et al.* 2010; Blok *et al.* 2011; Macias-Fauria *et al.*
 92 2012; Myers-Smith *et al.* 2015a); however, new recruitment (Lantz, Gergel & Henry 2010a;
 93 Boulanger-Lapointe *et al.* 2014; Büntgen *et al.* 2015), rather than growth alone, will drive shrubline
 94 advance. Thus, it is still uncertain if the same climate or biological drivers will control shrubline
 95 advance relative to shrub expansion in tundra ecosystems.
 96
 97 Treeline advance has been studied in more detail than changes in the elevation limit of tall shrub
 98 species, and the reported drivers of treeline advance, though often linked to climate, are varied
 99 (Harsch & Bader 2011). A global meta-analysis of 166 treelines found that over half had advanced
 100 in elevation since 1900, while just under half remained unchanged over the same period (Harsch *et*
 101 *al.* 2009). Climate sensitivity of tree growth has been identified at treeline (Ettinger, Ford &
 102 HilleRisLambers 2011); however, the controls on tree recruitment at treeline are often related more

103 closely to winter (rather than summer) weather and microenvironmental conditions (Wilmking *et al.*
104 2012; Hagedorn *et al.* 2014) or biotic interactions (HilleRisLambers *et al.* 2013). Shrubby treelines
105 such as the often low-statured mountain birch (*Betula pubescens* subsp. *tortuosa*) treeline have been
106 documented to be advancing in alpine ecosystems in Norway (Tømmervik *et al.* 2009; Hofgaard,
107 Dalen & Hytteborn 2009) and Sweden (Kullman 2002; Sundqvist, Björk & Molau 2008). However,
108 shrubline dynamics have been little studied relative to treeline advance, with only a few studies
109 investigating shrubline advance (Dial *et al.* 2007, 2016; Hallinger *et al.* 2010; Upshall 2011;
110 Rundqvist *et al.* 2011; Stöckli *et al.* 2011) and recruitment (Lantz *et al.* 2010a; Boulanger-Lapointe
111 *et al.* 2014; Büntgen *et al.* 2015) in tundra ecosystems (Fig. 1). Because shrubline advance is so
112 infrequently studied, we lack a complete understanding of the drivers of ecological boundaries
113 beyond treelines.

114

115 In this study, we tested the hypothesis that the willow shrubline has advanced over the past 50 years
116 in our focal research site in the Kluane region of the southwest Yukon Territory, Canada. We
117 compared largest stem initiation and growth rates to climate variables to test the climate sensitivity
118 of shrub recruitment and growth. If shrubline advance is related to a large-scale regional driver such
119 as climate, we predict consistent evidence of new recruitment across the study region. If shrubline
120 advance is mediated by local-scale processes, such as microclimate, herbivory or disturbances, we
121 predict variation in recruitment patterns across the region. We used dendroecology to investigate
122 shrub largest stem initiation over the second half of the 20th century and repeat ecological
123 monitoring over a four-year period (2009 - 2013) to calculate current, and estimate future, rates of
124 cover change, recruitment, age distributions and shrub densities at the elevational shrubline in this
125 high-latitude alpine tundra ecosystem.

126

127 **Materials and Methods**

128 *Literature Review*

129 We surveyed the literature for all studies presenting evidence of shrub dynamics including:
 130 patch/cover change, infilling or recruitment change in existing shrub tundra, and advance of the
 131 latitudinal or elevational shrubline (Fig. 1). We began with existing reviews of shrub expansion
 132 (Myers-Smith *et al.* 2011a; Büntgen *et al.* 2015) and then supplemented these literature reviews
 133 using the search terms: “tundra” and “shrubs” and conducting a comprehensive search for the years
 134 2011 to 2016 using both Web of Science and Google Scholar. We recorded the shrub change
 135 observed, coordinates of the study sites, species under investigation, methods used, sample size and
 136 other relevant information for all studies identified (Table S1).

137

138 *Field surveys*

139 We investigated shrubline advance along 26 hill-slopes in 14 sites in the Kluane region of the
 140 southwest Yukon Territory (Table S2, Fig. 3a, Fig. S1 and S2) from 2007 to 2009. The Kluane
 141 Region is located along the continental divide where the Pacific flora transitions into the Arctic
 142 flora (Cody 2000). Glacial refugia are thought to have been located in this region (Brubaker *et al.*
 143 2005), which could be a factor influencing the present-day variation in species composition (Fig.
 144 S2).

145

146 At each site, we established a survey transect parallel to the contours of the valley hill-slope at
 147 shrubline, the maximum elevation at which tall willow species grow (Fig. 2, Table S2). We
 148 searched for the highest elevation at which a plant from any of the tall willow species grew along
 149 the hill-slope. This individual became the first transect point and shrub to be surveyed along the
 150 shrubline transect. We identified each willow individual for each different species found within 3 m
 151 of a transect point located every 10 m along the hill-slope from the first shrub sampled, until we had
 152 sampled 8 individuals for age determination and growth ring width measurements. If no willows

were present at a given transect point, we walked further along or slightly down towards the shrubline transition until the next willow was reached. This survey method allowed for the distance among individuals and the density of shrubs at the shrubline ecotone to be calculated.

After surveying at shrubline, we walked down the hill-slope until reaching a subjectively estimated zone of approximately 50% tall willow shrub cover. At two sites, Burwash and Bison, cover was closer to 20% as the topography of the valley did not permit surveying on the same aspect at a lower elevation (Table S2). At all sites except Printers Pass and Copper Joe Creek, we repeated this survey on the opposite aspect of the valley or in the case Five Lakes on the opposite side of the ridge, and for Aishihik Ridge and Cranberry Ridge, at a location further along the ridge (Table S2).

The six most abundant tall willow species in the Kluane Region were *Salix pulchra* Cham. (diamond-leaf willow), *Salix niphoclada* Rydb. (barren-ground willow), *Salix glauca* L. Hook. (grey-leaf willow), *Salix richardsonii* Hook. (Richardson's willow), *Salix barrattiana* Hook. (Barratt's willow), and *Salix alaxensis* Andersson (felt-leaf willow, Table S3, Fig. S2). During the survey, we identified the species of each willow, and since these species are dioecious, we also identified the sex, if the individual had visible catkins (Myers-Smith & Hik 2012). When catkins were absent, we were not able to distinguish between the species *S. niphoclada* and *S. glauca* during field surveys. We have therefore combined these individuals into one taxonomic category; however, we believe that most individuals sampled in this group are *S. niphoclada*. Species identifications were confirmed by George Argus (Emeritus, National Herbarium of Canada). The location, elevation, hill-slope, and aspect were recorded, as well as the largest diameter of the shrub patch and the maximum height.

Climate data

178 The Kluane Region has a continental climate that is also influenced by coastal weather patterns with
 179 cold winters with October – February mean temperatures from -7°C to -15°C and relatively warm
 180 summers with June – July mean temperatures from 7°C to 11°C at lower elevations around 800m
 181 (Fig. S3). We used lapse rate corrected monthly Climate Western North America (ClimateWNA)
 182 v5.30 gridded temperature and precipitation data (4 x 4 km resolution, Wang *et al.* 2011) and
 183 Climate Research Unit (CRU) TS3.21 gridded temperature and precipitation data (0.5° resolution,
 184 Harris, Ian 2013). These climate data correlate well with local meteorological station data (Myers-
 185 Smith *et al.* 2015a).

186

187 *Sample collection*

188 We collected stem samples from 297 individuals across 20 of the 26 hill-slopes at 10 of the 14 sites.
 189 We collected a 3-5 cm sample of the largest stem of each individual for growth ring analysis just
 190 above the stem-root interface along two elevational transects on two hill-slopes for a total of eight
 191 individuals per transect and 32 individuals per valley (see above). Occasionally, samples could not
 192 be collected due to low shrub prevalence (e.g. Copper Joe Creek) or could not be processed due to
 193 wood rot or growth deformities, thus reducing the final sample sizes slightly at some sites (Table
 194 S2). Sampling was not conducted at the sites Aishihik and Cranberry Ridge, was only conducted at
 195 one aspect in Bison Valley, and at one elevation for Printer's Pass and Copper Joe Creek (Table
 196 S2). At two sites with longer continuous elevation gradients, Gladstones and Observation Plateau,
 197 we sampled again at a lower elevation where shrub cover was approximately 75% (Table S2).

198

199 In these alpine ecosystems near the elevational shrubline where shrub plants have few stems (from
 200 one to tens) and a stunted growth form, information from the base of the largest stem likely
 201 represents similar information to that found in the root collar, which may not be the case in more
 202 continuous shrub cover at lower elevations (Ropars *et al.* 2017). We restricted our sampling to
 203 higher elevations where willow patches were smaller and were non-contiguous in their extent (the

average willow patch diameter was 100 cm and the average density of individuals was 17 per 100m, Table S2), so that we were likely sampling only distinct genetic individuals. Although willow species can spread laterally through clonal growth, individuals growing in these extreme environments with shallow active-layer soil depths have been shown to be genetically distinct even when growing in relatively close proximity (Douhovnikoff *et al.* 2010).

Age estimates

Age estimates were determined for all samples using dendrochronology following methods adapted for tundra shrub species (Myers-Smith *et al.* 2015b). Rings were counted from thin cross sections of the largest stems harvested just above the root collar. The age of shrub stems was estimated as the maximum number of rings measured between four radii for each sample. We sampled two serial sections ~5 cm apart along the largest stem of 25 individuals and age estimates differed by 2 ± 0.5 years (mean \pm SE). We compared age estimates between the first and second largest stems on 18 different shrub individuals, and found that the stem age varied by an average of 6 ± 2 years (mean \pm SE) between these stems. Therefore, we assume that stem age estimates and the estimated initiation dates of the largest stem could have an error of around ± 6 years. Stem ages are only minimum estimates because sometimes rings are missing, the pith of the stem is rotten, or the largest stem or basal stem section might not represent the oldest part of the willow shrub. However, the estimated years of initiation of stems gives a good indication of the overall history of growth of these high-elevation shrubs.

Growth measurements

To process samples for annual radial growth measurements, we made thin sections of the shrub stems, mounted the sections on glass slides, and took digital images with a microscope mounted digital camera. Each shrub section was measured along four radii for annual increment with a resolution of $1\mu\text{m}$ (WinDendro, Québec, Canada or ImageJ, Research Services Branch, National

Institute of Mental Health, Maryland, USA). Each at 90° from the other unless the placement of radii had to be moved to avoid growth deformities or rotten wood, which occurred in approximately 10% of samples. To account for measurement error, we repeated the count for the first radii after completing the other three radii. Missing rings were accounted for during the visual crossdating conducted on the raw ring width measurements using marker rings such as the 2004 high growth year and the 2001 low growth year. We identified missing rings in 19% of samples of these repeated measurements. Willow stem sections varied in the ease at which rings could be counted and the information that these rings contained. A statistic of the repeatability of the measurement was calculated by correlating the ring width measurements between the two repeated radii. The repeatability correlations (Pearson's r) was greater than 0.8 for 96% of samples. The radii for each stem sample were averaged. A statistic of uniformity between the four radii was calculated for each sample by averaging the correlation for each radius with the mean of all four radii. Correlations (Pearson's r) among all of the sample radii were greater than 0.8 for 88% of the samples.

Growth data

We removed the first five years of growth to account for irregular growth patterns during early life stages. Data were not detrended to account for age-related growth, as these trends were not present in most shrub individuals and we wanted to treat all individuals in the same manner (Myers-Smith *et al.* 2015b). Growth data at the level of the individual and climate data at the site level were mean centred and variance scaled using the standard score to convert all growth and climate data into the same units and to meet the assumption of normality.

Shrubline Advance Estimates

Shrub densities were calculated from the sampling protocol as the number of shrub individuals encountered along the length of the sampling transect with a final unit of shrubs per 100 m of transect (Table S2). To calculate shrubline advance, we estimated the rate of change of shrub

density over time based on largest stem recruitment rates estimated from the dendroecological age estimates among the two transect elevations. This was calculated as the slope of the linear relationship between the number of shrubs per 100 m as recruitment progresses and time in years (see Fig S5). Thus, our estimates of shrubline advance assumed that hill-slopes with higher rates of shrubline advance had 1) greater rates of increasing shrub densities over time, and 2) greater differences in age distributions among transects at shrubline versus at lower elevations (Fig. S5).

Shrub cover change

We surveyed shrub cover, density, growth and recruitment in six 50 x 50 m plots at the Pika Valley site in July 2009 and 2013 following the Tall Shrub Monitoring Protocol (Myers-Smith *et al.* 2009). Clonal species can have extremely long lifespans and might not experience any age-related senescence over time (de Witte and Stöcklin, 2010); therefore, tundra willow patches, once established and growing in conditions with limited herbivory and stem dieback, can continue to expand for decades. We used willow densities calculated from distances among individuals, percent cover and patch sizes collected in the field surveys to quantify current and future tall willow cover.

Statistical analysis of age distributions

Statistics were conducted with the software R (version 3.2.2, R Development Core Team, Vienna). We used linear models to test for differences of shrubline advance and elevations between sites. We compared the minimum age of shrub individuals among sites using Kruskal-Wallis tests or between elevations among sites using Friedman rank sum tests using the package agricolae, because age distributions at high elevations were right skewed and non-parametric tests were required. We used mixed models with site as a random effect to test for a difference in patch width and height to compare the patch size of shrubs between sites. We used MANOVA and ANOVA to test for variation in patch size among species. We used a Shapiro-Wilk normality test to evaluate the age distributions. The variables stem width, patch width, patch height, and age were log transformed to

meet criteria for normality and homogeneity of variance. We used time series analysis to test the correspondence between pulses of largest stem initiation and weather data using the stats, mFilter and TTR packages (Büntgen *et al.* 2015). We used linear models to test the correspondence between detrended largest stem initiation (Hodrick-Prescott filter) and summer (June-July) and winter (October-February) temperature and precipitation data including one-year lags.

Statistical analysis of growth data

We used a linear mixed model analysis to quantify the climate sensitivity of growth (Myers-Smith *et al.* 2015b, a p.). Linear mixed models analysis can take into account hierarchical sampling structure, temporal autocorrelation and unbalanced sampling (Crawley 2007). Linear mixed models are growing in popularity in annual radial growth analysis because these models can account for variance in growth among years within individuals and variance among individuals within sites as well as heterogeneity in growth patterns over time of different individuals growing at the same site (Lapointe-Garant *et al.* 2010; Schmidt *et al.* 2010; Ettinger *et al.* 2011; Speed *et al.* 2011a; Subedi & Sharma 2013). We used the nlme package to conduct the mixed model analysis, using maximum likelihood estimation for model selection and restricted maximum likelihood estimation for slope estimates (Crawley 2007). We mean-centred and variance scaled all growth ring data at the individual level and climate data at the site-level prior to analysis, so that we can calculate the climate sensitivity among individuals at different sites. Our model structure included annual radial growth as the response variable, fixed effects included climate variables, and random intercepts for year and an autocorrelation structure (AR1, autoregressive process of order one). We calculated the conditional R^2 value for each mixed model using the r.squaredGLMM function of the MuMIn package (Nakagawa & Schielzeth 2013). We did not include random slopes in addition to random intercepts as this level of complexity led to singular convergences.

Model selection can be used to identify a single best model from a set of competing models (Johnson & Omland 2004). We tested 33 climate models chosen to represent the climate variables that we hypothesized would best explain the variation in annual radial growth and a null model. The 33 models included seasonal temperatures or precipitation variables and a selection of models with both temperature and precipitation variables. We used the same climate models as used by Myers-Smith et al. (2015a; sup. info) in a tundra biome-wide synthesis of annual radial growth data.

313

314 *Estimates of shrub cover change*

We used our collected age distribution, shrub cover and field survey data to make a simple projection of future patch expansion of tundra shrubs overtime across the Kluane Region. We used exponential relationships to project patch size increase with age, based on the change in patch size of currently existing shrub patches over a 50-year period, and compared these results to measured increases over a four-year period (2009 – 2013). The 95% quantile relationship was calculated using the quantreg package.

321

322 **Results**

Our literature review indicated few studies demonstrating shrubline advance and increased shrub recruitment at sites around the tundra biome (Fig. 1, Table S1). Only six other studies at five study sites investigated shrubline advance beyond current elevational limits of shrub species in addition to this study (Dial *et al.* 2007, 2016; Hallinger *et al.* 2010; Upshall 2011; Rundqvist *et al.* 2011; Stöckli *et al.* 2011), and none investigated shrubline advance beyond latitudinal limits of the species. Ten studies investigated recruitment of tundra shrubs. All of the above studies find some evidence for shrubline advance and increased recruitment at sites around the tundra biome (Table S1), with two of the studies indicating both increases and decreases or stable shrublines (Rundqvist *et al.* 2011) or recruitment rates (Boulanger-Lapointe *et al.* 2014).

332

333 Our field surveys of 379 individuals at 14 sites indicated that shrub density and the stature of tall
 334 willows decreased from treeline with greater elevation (Table S2). Our sampling of 297 of the
 335 surveyed individuals at 10 sites indicated skewed age distributions and younger willows at
 336 shrubline transects than in the zone of 50% shrub cover (Fig. 5 and Fig. S4; Friedman rank sum test
 337 = 14.22, $F_{2,144} = 64$, $P_{\chi^2} < 0.01$, $P < 0.01$). Ages at shrubline did not vary significantly between sites
 338 (Kruskal-Wallis $\chi^2 = 34.40$, $df = 36$, $P = 0.54$). Shrub density differed between sites (Table S2);
 339 however, all sites showed similar patterns of largest stem initiation and increasing density over time
 340 (Fig. S5). Only one case of mortality was observed in the survey of 379 individuals, and
 341 observations of stem mortality were very infrequent. When travelling between sites, only three dead
 342 individuals were observed, with evidence of stem girdling present in each case, likely as a result of
 343 small mammal herbivory. The rates of shrubline advance (Fig. 3a) and elevation of shrubline (Fig.
 344 S1) varied across the Kluane Region. Shrubline advance was negatively correlated with the hill-
 345 slope of the alpine valleys (Fig. 3a) and was not explained by aspect and elevation (linear model, P
 346 = ns). Willows were smaller at shrubline relative to those found at lower elevations (Table S2,
 347 linear mixed models, shrubline estimate \pm SE = -0.44 ± 0.06 m, t -value = -7.39 , $P < 0.01$).
 348

349 Tall willow diversity was variable across the Kluane Region with different willow species growing
 350 at the shrubline ecotone (Fig. S2). However, three species, *S. niphoclada*, *S. pulchra*, and *S.*
 351 *richardsonii*, were most abundant and made up ~ 80% of all the individuals sampled. Age among
 352 all willow species surveyed did not differ significantly (Kruskal-Wallis, $\chi^2 = 60.74$, $df = 51$, $P =$
 353 0.17). Patch sizes, measured as both width and height, varied between species (MANOVA, Pillai's
 354 trace = 0.25 , $F_{10,564} = 7.91$, $P < 0.01$) and this was due to variation in the growth form of the more
 355 rarely sampled species. *Salix alaxensis* individuals grew taller, and *S. barratiana* individuals were
 356 generally shorter in stature than the other species. No differences were observed in height of the
 357 three most commonly surveyed species (ANOVA, $F_{2,224} = 1.39$, $P = 0.25$); however, patch sizes
 358 were larger for *S. pulchra* (ANOVA, $F_{2,224} = 8.61$, $P < 0.01$, Tukey's Test pair-wise comparisons).

359

360 Largest stem initiation pulses were correlated with winter temperatures (Fig. 5) and the variation in
 361 annual radial growth of willows was best explained by summer temperatures (Fig. 6, Fig. S6, Table
 362 S4). Climate sensitivity of willow annual radial growth was variable across the Kluane Region (Fig.
 363 6, Fig. S6, Table S4) and this variability was not explained by hill-slope, elevation or species
 364 composition (linear mixed models, $P = \text{ns}$). We observed shrub recruitment rates of $\sim 20 \pm 5$
 365 individuals per hectare per decade (mean \pm SE) and measured rates of increased shrub cover of $\sim 5 \pm$
 366 1% per decade (mean \pm SE) from seedling and patch expansion surveys at the Pika Camp site over
 367 the period 2009 to 2013. Using a simplified relationship between age and patch size constrained by
 368 the monitoring data, and based on the assumption that conditions will remain similarly favourable,
 369 we estimated that willow cover will increase by at least 20 percent at lower elevations and could
 370 increase as much as five-fold at the shrubline ecotone over the next 50 years (Fig. 7).

371

372 **Discussion**

373 This study provides compelling evidence for wide-spread recent advance of the shrubline across
 374 high-latitude alpine tundra of the Kluane Region. While it is commonly assumed that there is ample
 375 evidence for shrubline advance in tundra ecosystems eg. IPCC Working Group II (2014), studies
 376 documenting shrubline advance or increasing shrub recruitment are rare (Fig. 1, Table S1). In the
 377 Kluane Region, we found uniform patterns of increases in the initiation of the largest stems among
 378 species and sites with differing aspects and hill-slopes. This indicates that a regional driver such as
 379 climate warming is likely to be responsible for the observed changes. Annual radial growth of these
 380 willow species was best explained by interannual variation in summer temperatures, and pulses of
 381 initiation of the largest stems by winter temperatures. A previous literature review of recruitment
 382 rates of tundra shrubs did not identify a consistent timing of increased recruitment at sites around
 383 the tundra biome (Büntgen *et al.* 2015).

384

385 In the Kluane Region, the earliest pulse in the initiation of the largest stems of shrubs at shrubline
 386 occurred between 1989 and 1996, and began earlier, between 1980 – 1985, in the 50% shrub cover
 387 zone (Fig. 4). Summer temperatures have been warming gradually in the region since 1960 and
 388 general increase in winter temperatures have occurred since the early 1980s (Fig. S3). We observed
 389 almost no dead individuals, and saw little evidence of dieback or dead stems in the field surveys,
 390 indicating that adult willow mortality has been very low in recent years. In cold tundra
 391 environments, woody material decomposes slowly (Hobbie 1996) and should be preserved on the
 392 landscape for decades. The observed high recruitment rates and low mortality, climate sensitivity of
 393 initiation of largest stems and growth indicate that a rapid change in shrub cover is currently
 394 occurring in alpine tundra of the Kluane region. If conditions remain favourable for growth and
 395 recruitment over the next 50 years, tall willow cover could increase by 20% or more and shrubline
 396 could continue to advance in this region (Fig. 7).

397

398 *Shrubline advance*

399 We suggest that climate warming has improved growth and recruitment conditions, leading to the
 400 observed increased shrub abundance and cover in the Kluane Region. We found a uniform pattern
 401 of shrubline advance between the four dominant tall willow species and an increasing rate of largest
 402 stem initiation across the Kluane Region. The age of willow stems was surprisingly uniform among
 403 sites and between species, with a median shrubline age of 17 years at the shrubline ecotone, despite
 404 variation in shrubline elevation. Rapid advance of white spruce treeline (*Picea glauca*) on south-
 405 facing hill-slopes and stable treelines on north-facing hill-slopes have been observed in this region
 406 (Danby & Hik 2007). However, we observed no variation in age, height or advance of shrubline
 407 with valley aspect. Our results indicate a contrasting importance of microclimate for treeline versus
 408 shrubline advance in this region, and that regional factors are more important than local factors as
 409 drivers of shrubline advance.

410

411 *Climate warming*

412 Our results suggest that growth and initiation of largest stems are controlled by different climate
 413 variables in the Kluane Region. Annual radial growth of willows correlated best with summer
 414 temperatures, whereas pulses in the initiation of largest stems correlated best with winter
 415 temperatures. Climate has been identified as a significant factor influencing the growth (Forbes *et al.* 2010; Hallinger *et al.* 2010; Blok *et al.* 2011; Macias-Fauria *et al.* 2012; Tape *et al.* 2012;
 416 Elmendorf *et al.* 2012b; Weijers *et al.* 2012; Myers-Smith *et al.* 2015a p.) and establishment
 417 (Harsch *et al.* 2009; Van Bogaert *et al.* 2010; Harsch & Bader 2011; Mamet & Kershaw 2012) of
 418 woody species in northern alpine or tundra ecosystems. Summer temperatures could either
 419 negatively influence (Shevtsova *et al.* 2009) or promote (Graae, Alsos & Ejrnaes 2008; Milbau *et al.* 2009; Buntgen *et al.* 2015) seedling establishment, and winter temperatures and cold
 420 stratification can influence seed germination rates, seedling mortality and fungal infection (Graae *et al.* 2008; Wilmking *et al.* 2012; Hagedorn *et al.* 2014). In alpine ecosystems, where snow is
 421 redistributed by wind, seedlings may be exposed to atmospheric temperatures rather than being
 422 protected by an insulating snow pack and thus increasing winter mortality on exposed ridges (Wipf,
 423 Stoeckli & Bebi 2009; Myers-Smith & Hik 2013).

427

428 Factors other than climate, such as cold-induced photoinhibition, permafrost disturbance, herbivory
 429 or plant–plant interactions, could also influence growth and recruitment at elevational treelines and
 430 shrublines (Harsch *et al.* 2009; Myers-Smith *et al.* 2011a; HilleRisLambers *et al.* 2013). In the
 431 Kluane Region, shallow alpine tundra soils are underlain by bedrock, and thus permafrost thaw will
 432 likely have less influence on surface conditions and shrub recruitment or productivity relative to
 433 other tundra environments (Natali, Schuur & Rubin 2012; Wilmking *et al.* 2012). Signs of
 434 herbivory on shrubs are low in the Kluane Region relative to other tundra ecosystems (Christie *et al.* 2015; Barrio *et al.* 2016). The major herbivores on tundra shrubs include ptarmigan browsing
 435 new buds in spring, non-cyclic insect herbivores, stem herbivory by small mammals including

marmots and rare browsing by moose or other large herbivores. Although not the focus of this study, we believe that herbivory is unlikely to be a major limiting factor for shrub expansion currently in the Kluane Region. In summary, our results point to climate as a driver of shrub expansion and shrubline advance in the Kluane Region.

Similar to our observations for shrublines, treeline advance has been documented in the Kluane Region and has been attributed to summer warming (Danby & Hik 2007). Summer temperatures have increased by approximately 1°C between 1980 and 2010 in the Kluane area (Fig. S3), and this warming is likely linked to the climate regime shifts observed in the North Western Pacific in 1977 and 1989 (Hare & Mantua 2000). Sporadic pulses of recruitment are a common phenomenon at treeline (Körner 2012), however age distributions of tall willow species in this study indicate conditions for recruitment have gradually improved over the past half century. We found that pulses in largest stem initiation were best explained by variation in winter temperatures indicating that frost damage might be a driver of seedling mortality. We predict that if recruitment conditions continue to remain favourable, increased recruitment will continue to occur in this region.

Disturbance

Disturbance can influence recruitment rates in tundra ecosystems. Fire (Lantz *et al.* 2010a, 2013) and permafrost degradation (Lantz *et al.* 2009) have been positively associated with recruitment in alder in the Western Canadian Arctic (*Alnus viridis* subsp. *fruticosa*) and caribou trampling has been associated with increased recruitment of *Betula glandulosa* in Northern Quebec (Ropars & Boudreau 2012). In contrast, herbivory can limit the advance of woody species up hill-slopes in northern mountainous regions (Cairns & Moen 2004; Olofsson *et al.* 2009; Hofgaard *et al.* 2009; Van Bogaert *et al.* 2010; Speed *et al.* 2010, 2011b, 2012) and shrub encroachment in tundra ecosystems has been shown to be reduced or inhibited by herbivores (Post & Pedersen 2008; Olofsson *et al.* 2009; Tape *et al.* 2010; Christie *et al.* 2015). Various animal species feed on willow

463 shrubs ranging from large herbivores such as caribou and reindeer (Olofsson *et al.* 2009; Forbes *et*
 464 *al.* 2010; Zamin & Grogan 2013; Bernes *et al.* 2015), birds such as ptarmigan (Tape *et al.* 2010),
 465 small mammals such as voles and lemmings (Predavec & Danell 2001; Olofsson *et al.* 2009), and
 466 herbivorous insects (Olofsson & Strengbom 2000; Den Herder, Virtanen & Roininen 2004).
 467 Herbivory can influence both the establishment of new recruits and reduce the survival of adults.
 468 However, the impacts of herbivory on recruitment will likely have a larger influence on the
 469 population age structure (Speed *et al.* 2010).

470

471 In the Kluane Region, herbivore damage causing shrub death was only observed once in surveys of
 472 hundreds of willow individuals. Because seedlings are small and difficult to observe, we likely
 473 under-sampled willows younger than ~10 years, and therefore we might not have entirely accounted
 474 for seedling and sapling mortality. Willow seeds have variable and often low germination rates
 475 (Shevtsova *et al.* 2009; Graae *et al.* 2010), and therefore studying the factors promoting recruitment
 476 in these species is logistically difficult. It is likely that in addition to winter temperatures, growing
 477 season conditions, disturbance regimes, nutrient availability, seed quality, seed production, other
 478 reproductive factors, and variable herbivory could all interact to determine the new recruitment of
 479 willow species. However, increasing recruitment in recent decades suggests that herbivory on
 480 seedlings or other sources of mortality are not currently a major limiting factor of shrubline advance
 481 in the Kluane Region.

482

483 *Limits to shrubline advance*

484 Our results indicate that the initiation of the largest stems of tall willows and shrub cover have
 485 increased and will likely continue to increase, if growing conditions remain the same or continue to
 486 improve as long as other factors do not become limiting. However, quantitatively projecting future
 487 shrubline advance in this region is more difficult. Shrub growth and patch expansion is limited by
 488 available resources (Tape *et al.* 2012), and shrubline advance is limited by factors such as substrate,

seed source and disturbance. Large-scale disturbances such as hill-slope erosion were observed at many of the sites that had low elevation shrublines. Hill-slopes with talus, scree or exposed rock are not sufficiently stable at higher elevations to support further willow range expansion. On many of the hill-slopes with high shrublines, tall willows are already growing close to the tops of ridges. Though these shrubline individuals were small in stature and did not make up a significant proportion of the overall shrub cover, they had successfully established and were persisting at these higher elevation sites.

We observed low reproductive effort and potential pollen or resource limitation in these individuals (Myers-Smith, Saunders and Hik, unpublished data). Inadequate successful reproduction is one of the common demographic explanations for range limits (Gaston 2009). Willows growing at the highest elevations in Kluane might not be reproductive and many established seedlings at the shrubline ecotone could come from seed sources located further down the hill-slope. Reproduction could improve with age allowing greater recruitment of individuals from seeds produced at high elevations in the future. Although we predict further increase in cover of willow shrubs in this region, shrubline advance could be limited by active disturbance, available soil substrates, seed source and poor high-elevation reproduction.

Conclusions

Our findings add to the growing evidence of increases in shrub abundance in tundra ecosystems, and provide one of the few examples of both upslope advancement and increasing rate of initiation of largest stems of shrubs in relation to climate warming in tundra ecosystems (Fig. 1). We find that contrasting seasons influence growth (summer) and largest stem initiation (winter) in this system. A significant change in tall shrub canopy cover and elevational range extent will begin to alter a variety of factors from soil temperatures and nutrients (Blok *et al.* 2010; Buckeridge *et al.* 2010; Myers-Smith & Hik 2013) to habitat availability for tundra-dwelling animal species (Wheeler &

Hik 2013; Boelman *et al.* 2015), which could feedback to influence tundra ecosystem functions as a whole. If growing conditions remain the same or improve over the next 50 years, we predict that tall willow cover will increase by at least 20% and enhanced recruitment will continue to lead to further shrubline advance. However, our results highlight that with different climate drivers for growth and recruitment, variation in the rates of future climate change between summer and winter seasons could lead to different trajectories for vegetation dynamics in this high-latitude alpine tundra.

Authors' contributions

IMS and DH conceived the study; IMS collected and analysed the data; IMS wrote the paper with contributions from DH.

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541 **Data Accessibility**

542 Data are available at the polar data catalogue (<https://www.polardata.ca> Reference Number = 1647).

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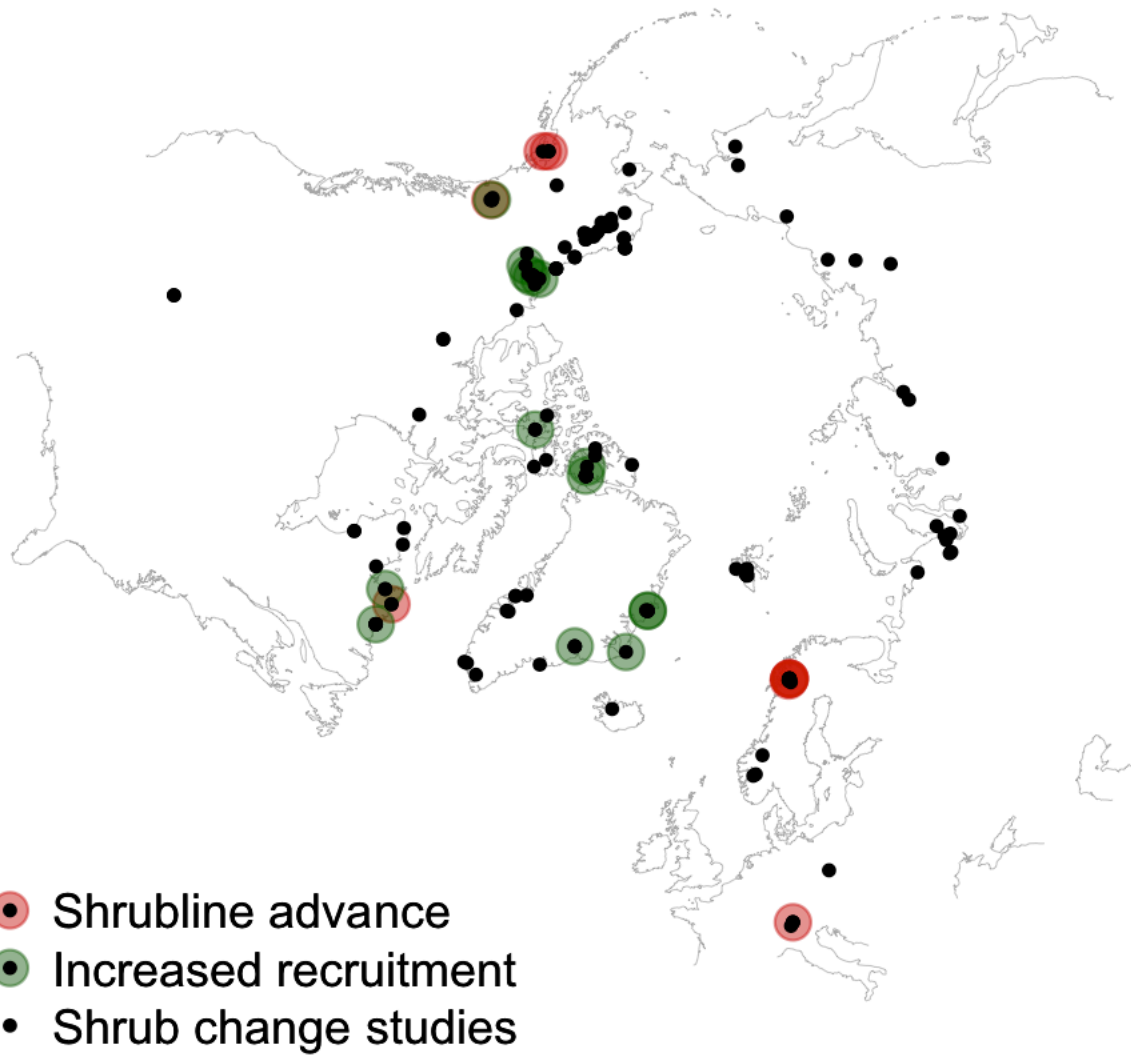
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- 923

Figures



025

026 Figure 1. Evidence of shrubline advance (red), increased recruitment (green) from the 60 studies of
 027 shrub change and 128 study locations at sites around the tundra biome identified in the literature. Six
 028 studies at five study sites investigated shrubline advance beyond current elevational limits of shrub
 029 species in addition to this study, and none investigated shrubline advance beyond latitudinal limits of
 030 the species. Ten studies investigated increased recruitment.

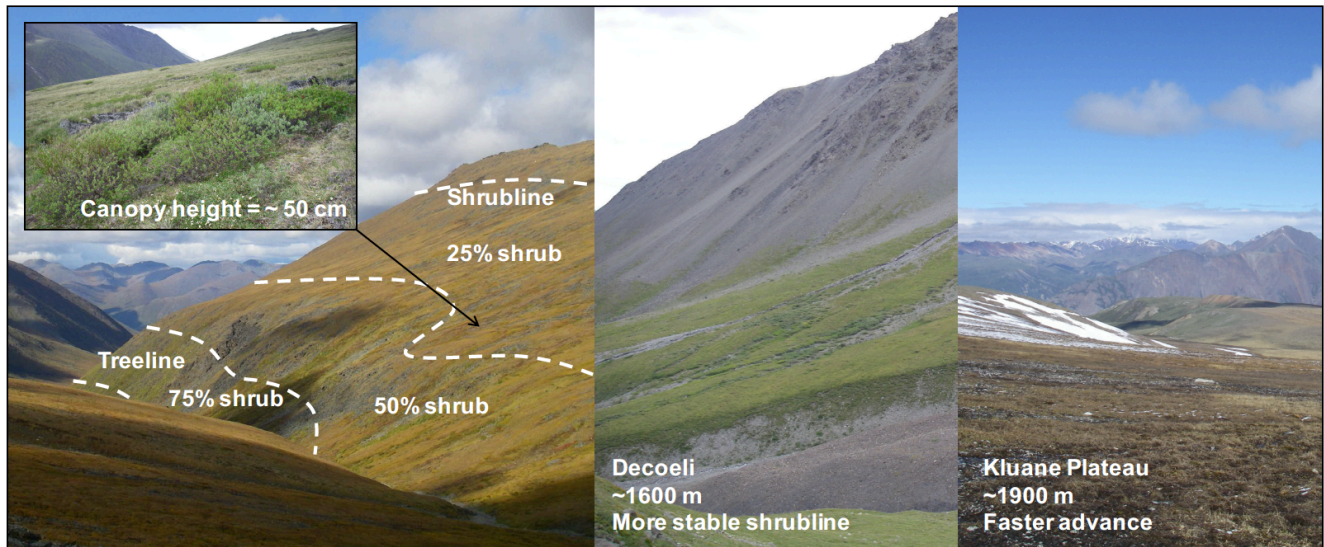


Figure 2. Elevational shrub densities from treeline to shrubline (the maximum elevational extent at which tall shrubs grow) in the Kluane Region of the Southwest Yukon. At treeline willow shrubs can reach over 2m tall, at the 50% shrub zone canopy heights are around 50 cm, at shrubline canopy heights are often 30 cm or lower (Table S2). The hill-slopes and soil substrate vary across the region with more stable shrublines being found on steeper hill-slopes (such as the west-facing Decoeli hill-slope pictured here with a shrubline of approx. 1600 m) and faster-advancing and higher shrublines being found on shallower hill-slopes (such as the north-facing Kluane Plateau pictured here with a shrubline of approx. 1900 m).

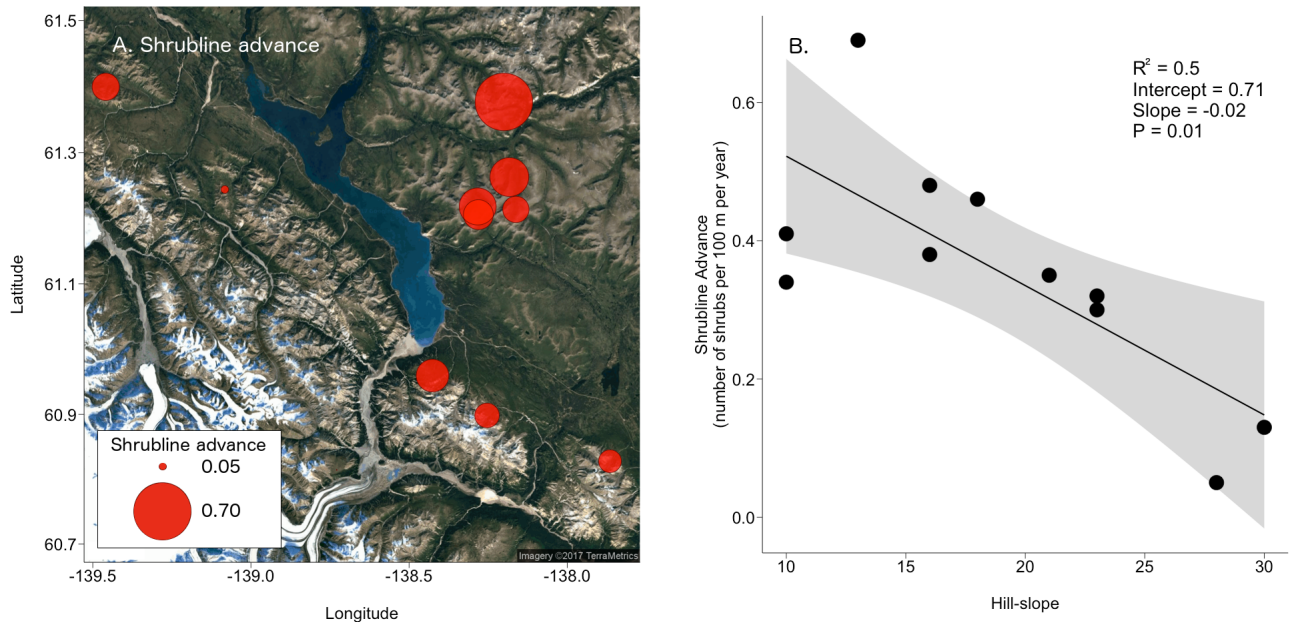
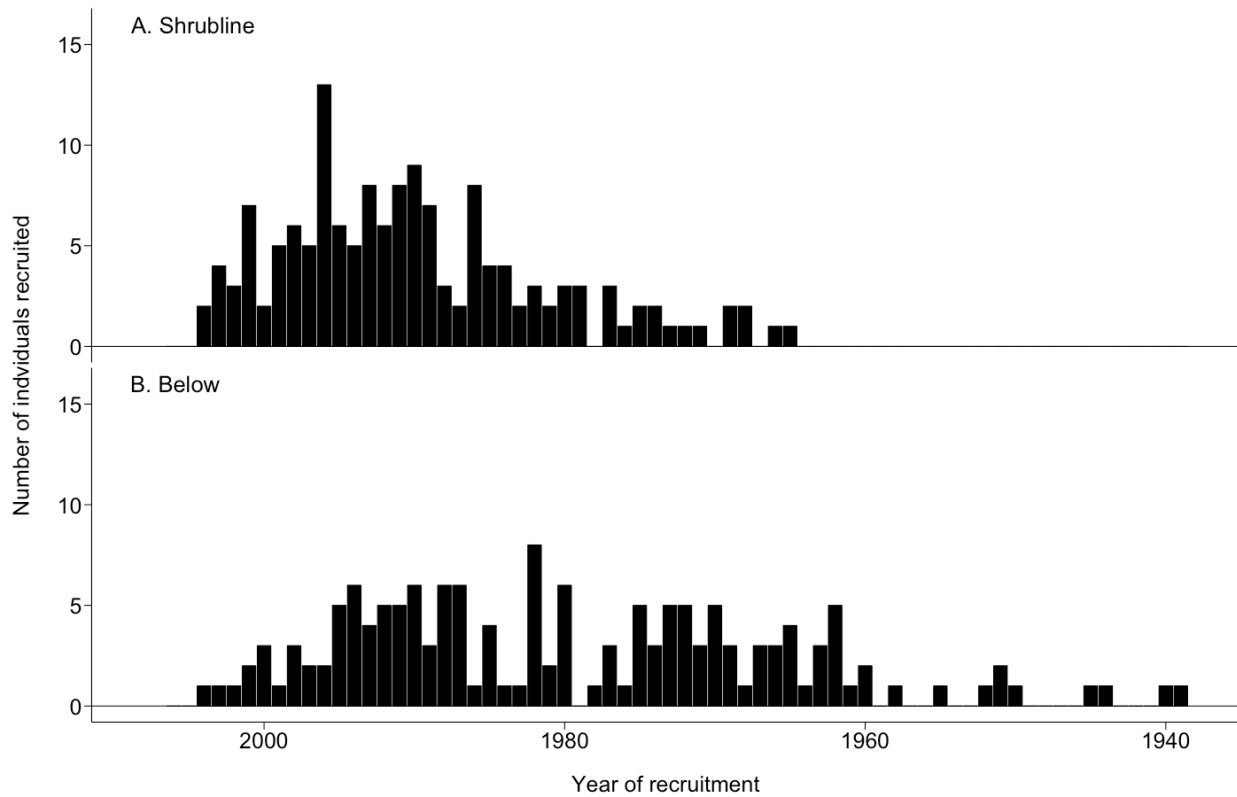


Figure 3. Evidence of shrubline advance (slope of the relationship between the number of shrubs per 100 m as recruitment progresses and time in years, see Fig S5) at sites across the Kluane Region of the Southwest Yukon. Shrublines that are advancing faster (a greater increase in shrub density over time) are indicated by larger red circles (A). Shrubline advance was higher for sites with more shallow hill-slopes across the 11 alpine valleys studied (B). Hill-slope was the only measured topographic or ecological variable that explained variation in shrubline advance among the 11 study sites.



047

048 Figure 4. Age distributions indicate that shrublines are advancing in the Kluane Region of the
 049 Southwest Yukon. Age distributions of willows at (A) and below (B) shrubline are pooled for all sites
 050 at the shrubline and 50% shrub ecotones. The distribution of willows at shrubline is right skewed
 051 indicating a higher proportion of younger individuals at the shrubline ecotone (Shapiro-Wilk normality
 052 test, $W = 0.94$, $P < 0.01$).

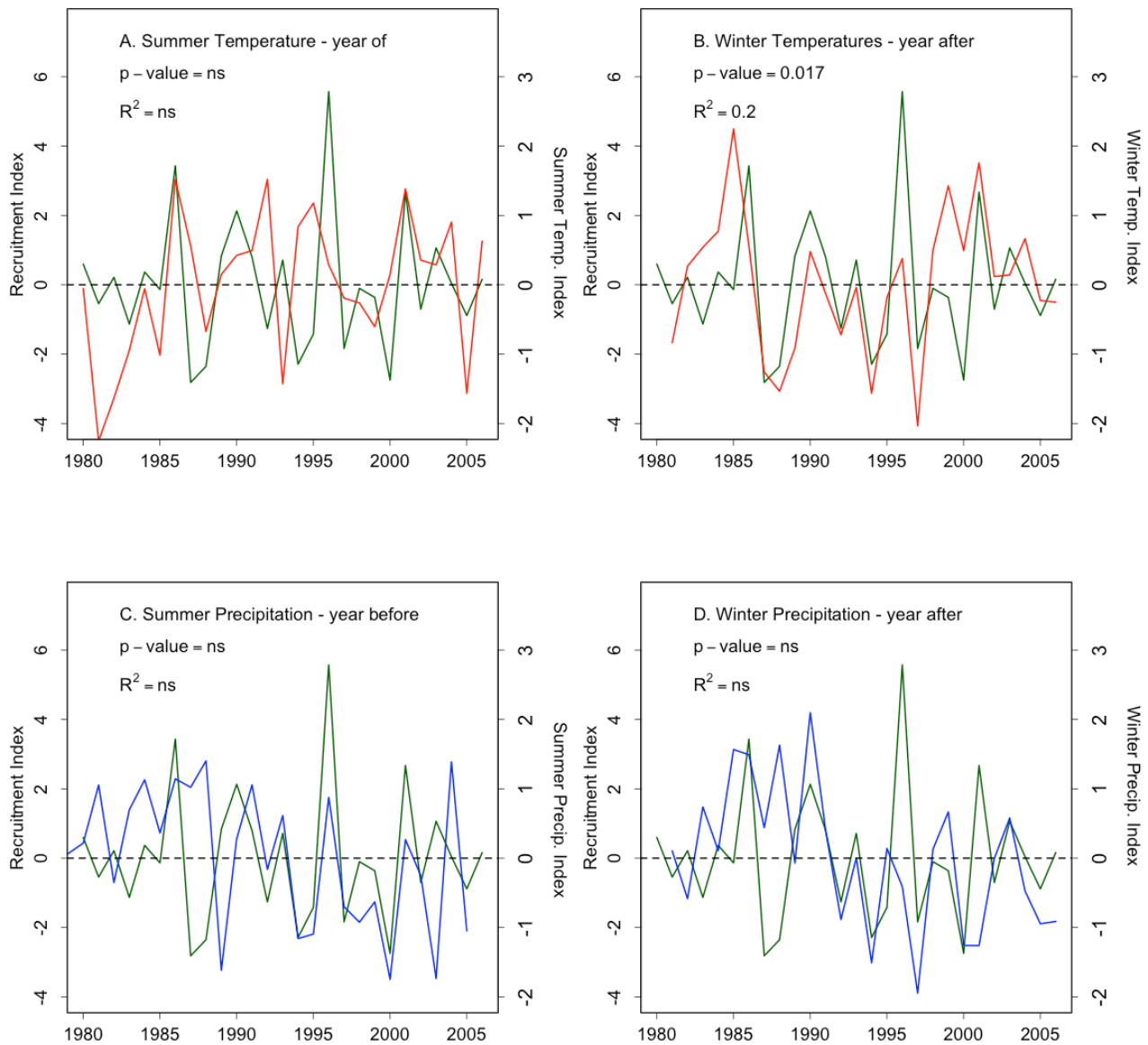


Figure 5. Variation in willow recruitment at the elevational shrubline plotted as a detrended index from the time series analysis (green) in the Kluane Region of the Southwest Yukon is best explained by winter temperatures the year after germination (B). The red lines in plots A and B indicate the June – July mean and October – February mean temperatures and the blue lines indicate precipitation over the same periods. Climate data are CRU TS3.21 gridded temperature and precipitation data (0.5° resolution).

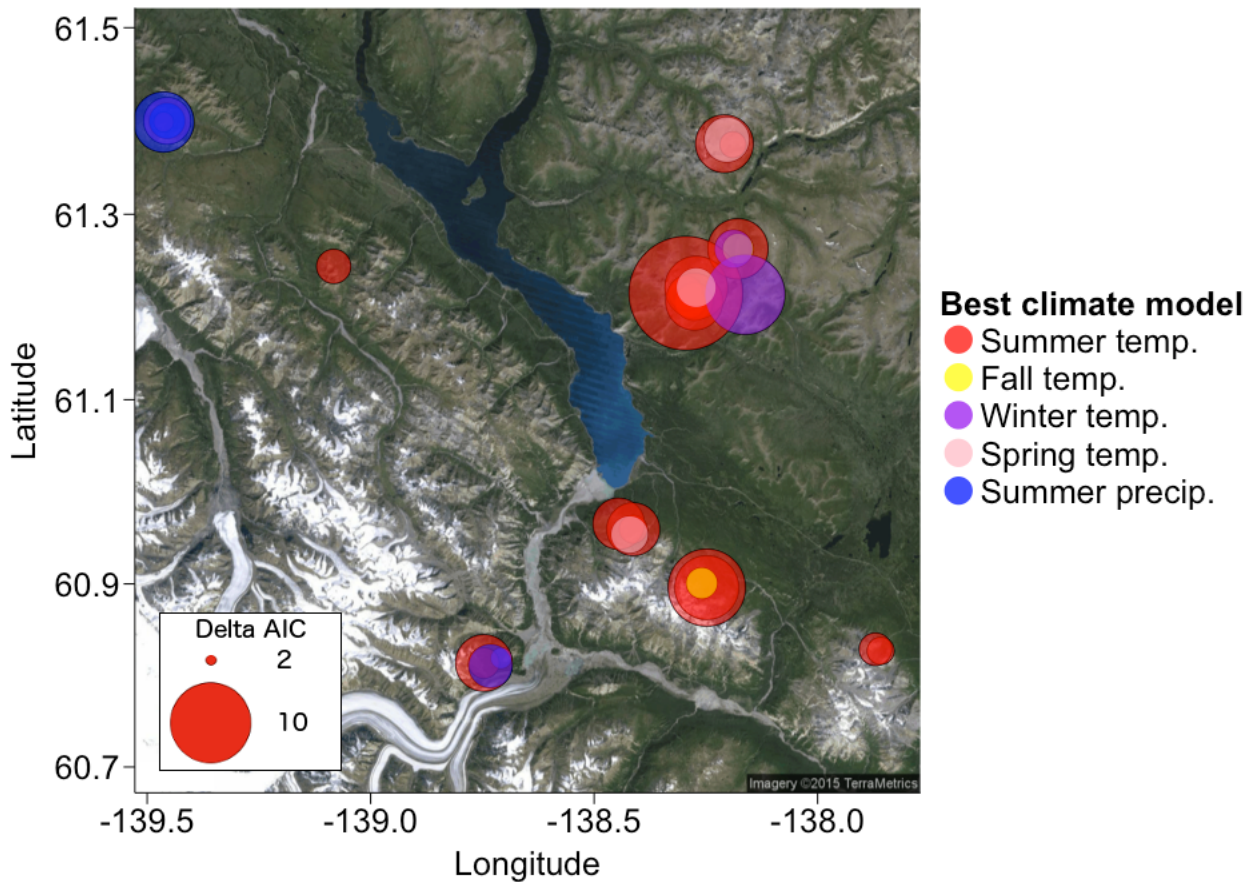
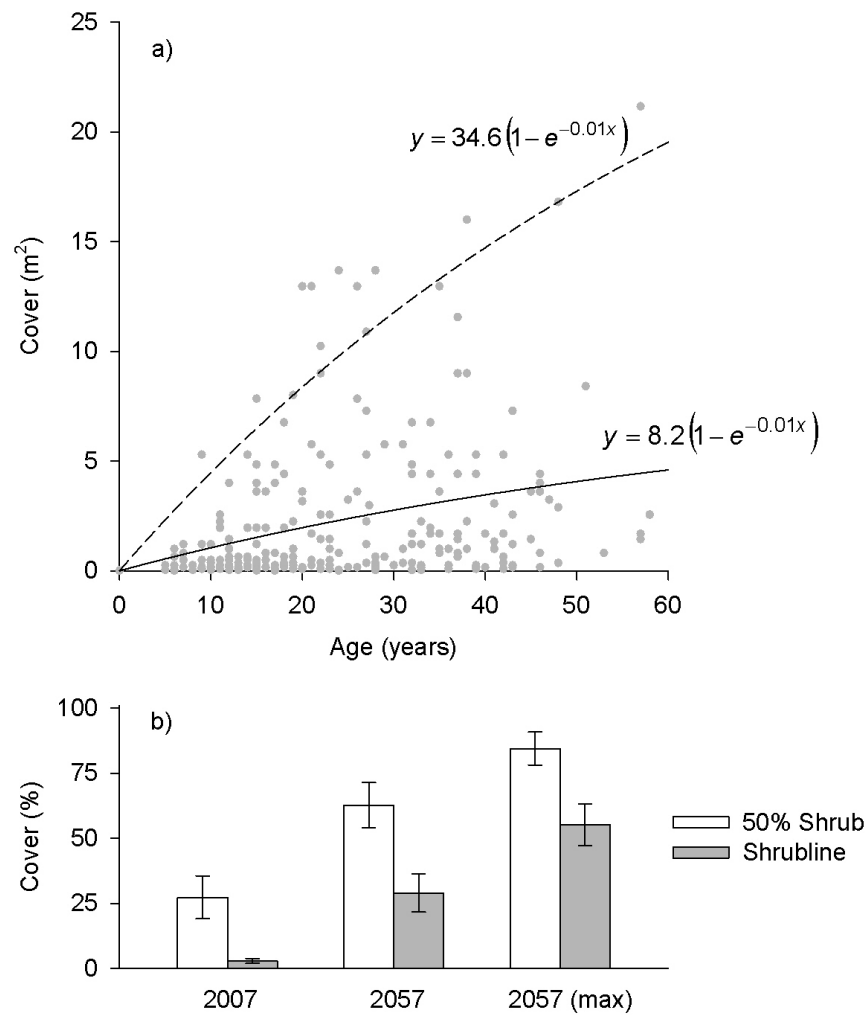


Figure 6. Map of climate sensitivity of growth of willows across the Kluane Region of the Southwest Yukon. Summer temperatures best explained the variation in shrub growth at most sites. The size of the circle indicates the strength of the climate sensitivity (ΔAIC value, see Figure S5 for other indices of climate sensitivity); colour indicates the type of climate model that best explained the variation in growth. Climate data are ClimateWNA v5.30 gridded temperature and precipitation data (4 x 4 km resolution).

Figure 6.



069

070 Figure 7. Estimated current and future projected tall willow cover in alpine tundra of the Kluane
 071 Region of the Southwest Yukon. The solid line is the exponential regression between patch age and
 072 shrub cover indicating the average growth rate and the dashed line is the 95% exponential quantile
 073 regression indicating the estimated maximum growth rate (a). The error bars (b) indicate the standard
 074 error of the projections for the shrub patch cover increases from the survey data, but not the overall
 075 uncertainty of these simplified model estimates which would be much greater. These estimates suggest
 076 that shrub cover will double at lower elevations and increase 10-fold at the shrubline ecotone, if
 077 conditions remain unchanged and all the individuals surveyed continue to grow at the same rate over
 078 the next 50 years (b). New recruitment and continued improved growing conditions, which are not

incorporated into this simple projection, are likely to result in an even greater rate of increase if rates of mortality, stem dieback and herbivory remain low. However, lack of suitable substrates further upslope may limit shrub expansion.

